

New Records of Fishes from Johnston Atoll, with Notes on Biogeography¹

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ABSTRACT: Thirty new records of fishes are reported from Johnston Atoll. Three are Hawaiian endemics, six are widespread Indo-Pacific species that reach Johnston but not Hawaii, and the remainder are widespread species that have been recorded from Hawaii and elsewhere in the Pacific. The number of fish species recorded from Johnston is raised to 301. The attenuated nature of Johnston's fish fauna may be due to several factors, including isolation, lack of habitat area and diversity, and glacioeustatic extinctions.

JOHNSTON ATOLL (16° 45' N, 169° 30' W) is one of the most isolated atolls in the world, 800 km south of the nearest reef of the Hawaiian Islands (French Frigate Shoals), 1500 km from the Line Islands to the southeast, and 2400 km from the Marshall Islands to the southwest (Figure 1). Geologically, Johnston is considered a part of the Line Islands chain, a 4200-km bathymetric feature stretching from Horizon Guyot (north of Johnston) to the northern end of the Tuamotu chain. Johnston's estimated age of 85 Ma is inferred from K-Ar ages of neighboring seamounts (Schlanger et al. 1984, Keating 1985). Johnston is thus older than Meiji Guyot, the oldest portion of the Hawaiian-Emperor chain still extant on the Pacific Plate (Grigg 1988). Like the rest of the Line Islands chain, Johnston was formed by alkalic volcanism typical of oceanic volcanism rather than midocean ridge activity, and a hotspot origin has been proposed. The exact mechanism and number of volcanic episodes involved are still debated (Schlanger et al. 1984).

Eight scientific collections of fishes resulting in published species lists have been made at Johnston over the past century. The earliest studies used line fishing, ichthyocides, and explosives to collect specimens (Smith and Swain 1883, Fowler and Ball 1925, Schultz et al. 1953–1966, Halstead and Bunker 1954). More recent studies have used divers (Gosline 1955, Brock et al. 1965) and submersibles (Randall et al. 1985, Ralston et al. 1986) to observe and collect specimens. The most comprehensive of these works (Randall et al. 1985) listed a total of 271 species known to occur at Johnston.

The focus of collecting efforts for the present study was the relatively unexplored depth zone between 25 and 75 m, deeper than previous diver collections and shallower than the majority of submersible observations. Collections for this study were made in June 1988 (R. Kosaki, R. Pyle, and S. Jazwinski), August 1988 (R. Kosaki and D. Irons), November 1988 (R. Kosaki), January 1989 (R. Kosaki and D. Irons), and August 1989 (R. Kosaki, D. Irons, and K. Kavanagh). Collection methods included rotenone, quinaldine, spears, hand nets, and line fishing. All specimens were deposited in the Bernice P. Bishop Museum, Honolulu (BPBM). The families are listed in phylogenetic order following Randall et al. (1985). Within each family, genera and species are listed alphabetically. Lengths are listed as TL (total length) for moray eels (Muraenidae) and cusk eels (Ophidiidae); SL (standard length) is listed for all other fishes.

¹ Hawaii Institute of Marine Biology Contribution No. 828. Fieldwork on Johnston was partially supported by U.S. Army Contract DACA83-84-C-0019. Manuscript accepted 1 August 1990.

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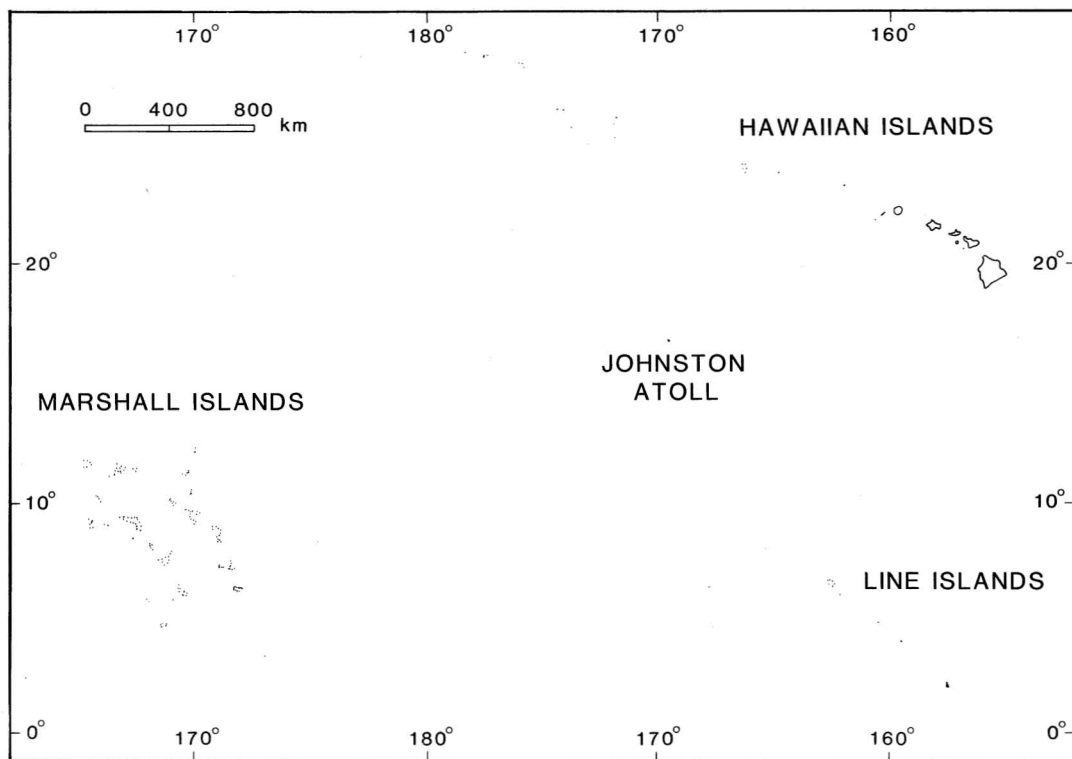


FIGURE 1. Map of the central Pacific showing Johnston Atoll and locations of the nearest island groups.

ANNOTATED LIST OF NEW RECORDS

Family MURAENIDAE

Enchelycore pardalis (Temminck & Schlegel, 1846)

BPBM 33965 (1 : 334 mm), Figure 2

One specimen collected with hand nets along a ledge at 35 m depth on the southwest edge of the lagoon platform. Another individual was seen by S. Jazwinski at 25 m depth outside the north side of the reef. Common in the Northwestern Hawaiian Islands and Japan, this species is relatively rare in the main Hawaiian Islands and at Johnston.

Gymnothorax margaritophorus Bleeker, 1865
BPBM 33990 (1 : 93 mm), Figure 3

This species is known from the Society Islands to South Africa, and north to the Ryukyu Islands. Not recorded from Hawaii.

Gymnothorax zonipectis Seale, 1906

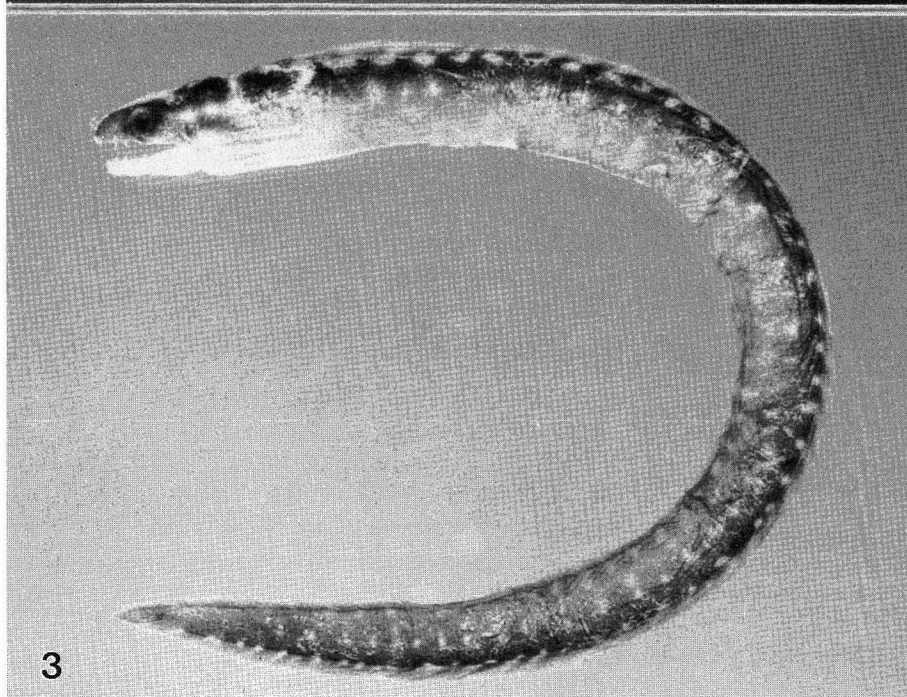
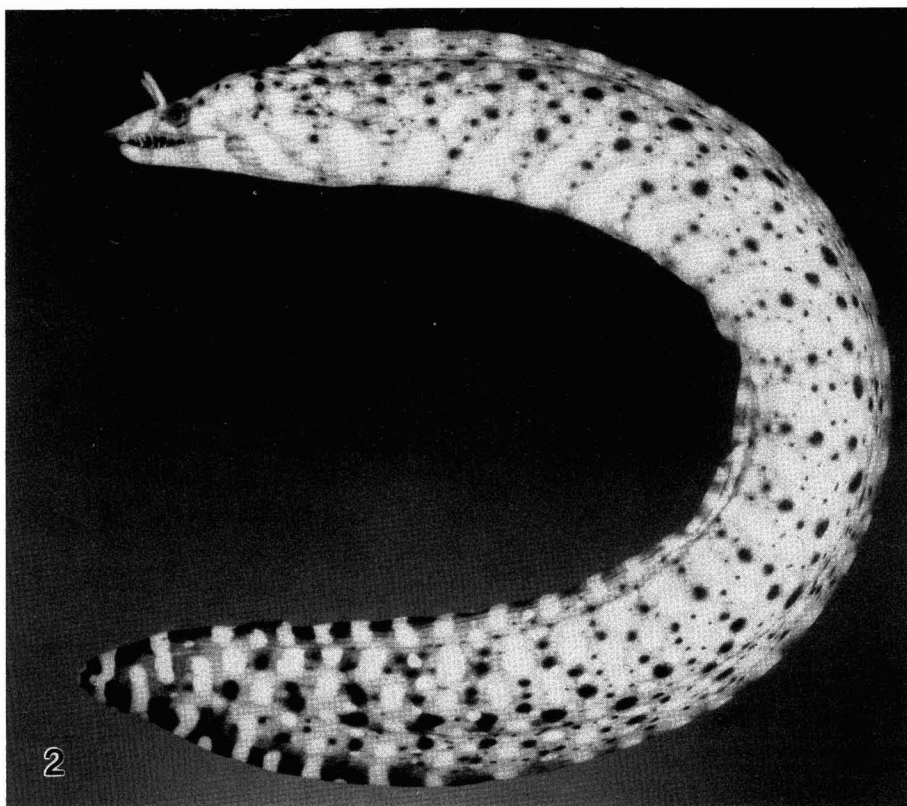
BPBM 34031 (1 : 106 mm)

Widespread on the Pacific Plate. Also known from Taiwan, Indonesia, and the Chagos Archipelago. Not recorded from Hawaii.

Siderea sp.

BPBM 33991 (1 : 120 mm); BPBM 34031 (1 : 171 mm)

Both specimens of this whitish moray strongly resemble an unidentified species that has been collected in the Persian Gulf, the Coral Sea, and in Papua New Guinea. The taxonomic status of these specimens remains unresolved at this time, but they are clearly distinct from *Siderea picta*, the only other member of this genus recorded from Johnston.



FIGURES 2-3. 2, *Enchelycore pardalis*, BPBM 33965; 3, *Gymnothorax margaritophorous*, BPBM 33990.

Family OPHIDIIDAE

Brotula multibarбата Temminck & Schlegel, 1846

BPBM 34013 (1 : 254 mm), Figure 4

One specimen collected with rotenone at 10 m depth outside the reef.

Family ANTENNARIIDAE

Antennarius coccineus (Cuvier, 1831)

BPBM 33971 (2 : 56 + 72 mm), Figure 5

This protectively colored species was collected with rotenone at 10 m depth outside Mustin Gap. One of the most widespread of the frogfishes, *A. coccineus* is recorded from East Africa to Costa Rica (including Hawaii).

Family SCORPAENIDAE

Scorpaenodes hirsutus (Smith, 1957)

BPBM 33997 (4 : 29–42 mm)

An Indo-Pacific species that ranges from the Red Sea to Hawaii. Johnston specimens collected with rotenone at 30 m depth.

Scorpaenopsis fowleri (Pietschmann, 1934)

BPBM 33999 (1 : 20 mm), Figure 6; BPBM 34008 (1 : 23 mm); BPBM 34053 (1 : 19 mm)

Occurs from the Chagos Archipelago to French Polynesia and Hawaii. Collected with rotenone at 30 m depth. This small species is placed in *Scorpaenopsis* primarily on the lack of palatine teeth; further study may result in its placement in a new genus.

Family SERRANIDAE

Aporops bilinearis Schultz, 1943

BPBM 33980 (1 : 92 mm), Figure 7

Collected with rotenone at 12 m depth outside the reef. We follow Johnson (1983) in classifying this species and other fishes formerly placed in the family Pseudogrammatidae in the Serranidae.

Liopropoma collettei Randall & Taylor, 1988

BPBM 34000 (1 : 58 mm), Figure 8

A single specimen was collected at 12 m depth outside the reef north of Mustin Gap. Previously recorded from the Philippines,

Papua New Guinea, and several localities in the Hawaiian Islands. Two forms of this species are known, a western Pacific form and a Hawaiian form; the latter was collected at Johnston.

Plectranthias winniensis (Tyler, 1966)

BPBM 33937 (2 : 37 + 38 mm), Figure 9

Recorded at many localities from the Red Sea to Hawaii; the Johnston specimens were collected at 40 m depth with rotenone.

Pseudanthias bicolor (Randall, 1979)

BPBM 34002 (2 : 97 + 101 mm), Figure 10

Speared at 35 m depth outside the north edge of the reef; other individuals observed at similar depths.

Pseudanthias randalli (Lubbock & Allen, 1978)

BPBM 34001 (1 : 31 mm), Figure 11; BPBM 34026 (2 : 24–36 mm)

Moderately abundant along a highly eroded limestone ledge at 65–75 m depth, where these specimens (all female) were collected with quinaldine. No males of this sexually dichromatic species were observed or collected. Not known from Hawaii. Identification is tentative, as revisionary work is needed in the Anthiinae.

Family PRIACANTHIDAE

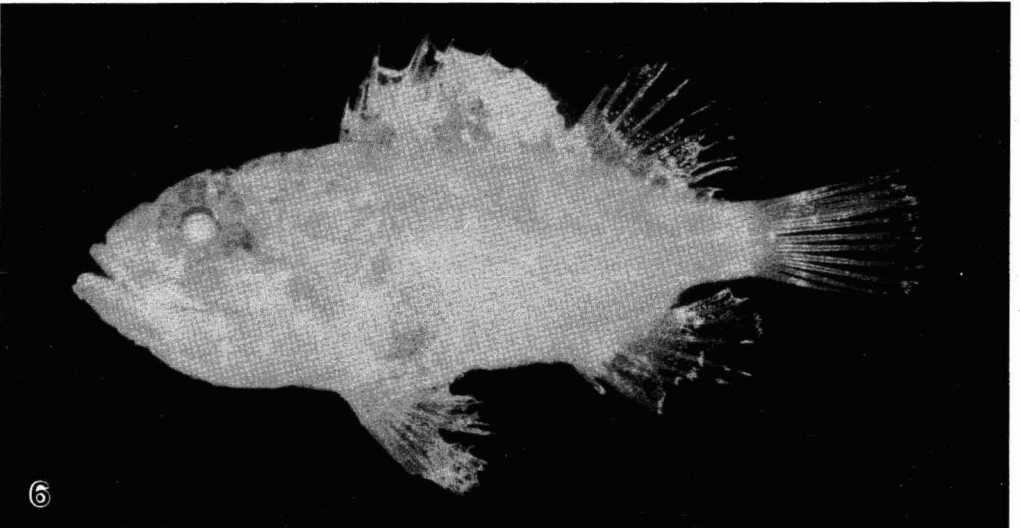
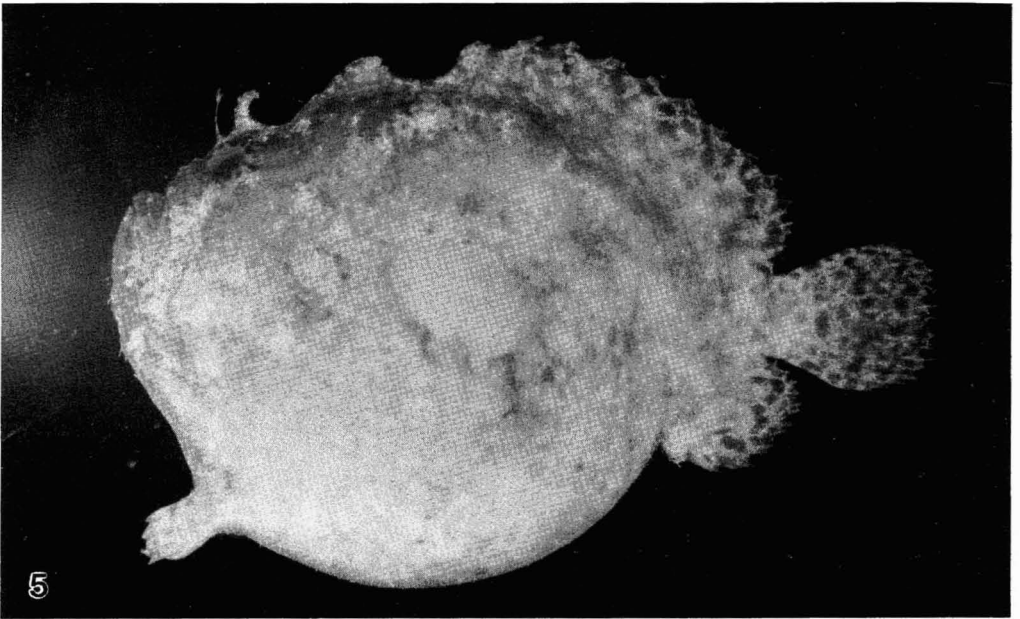
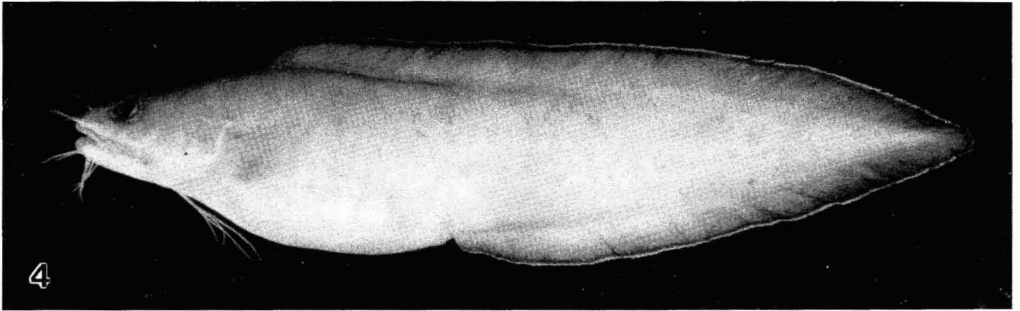
Priacanthus meeki Jenkins, 1903

A single specimen (210 mm) of this Hawaiian endemic was speared at 3 m depth at East Island; unfortunately, it was not retained. Of over 150 priacanthids taken by fishermen and examined by R. Kosaki and D. Irons, all were either *Heteropriacanthus cruentatus* or *Cookeolus japonicus* (*C. boops* of most authors, reported as a synonym of *H. cruentatus* by Starnes [1988]). *P. meeki*, thus, is probably a waif from the Hawaiian Islands.

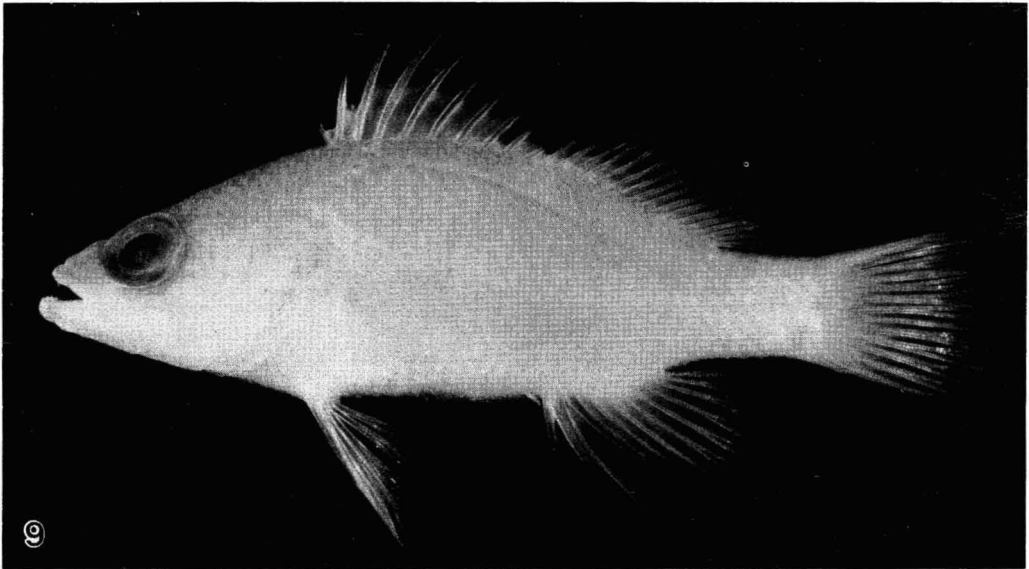
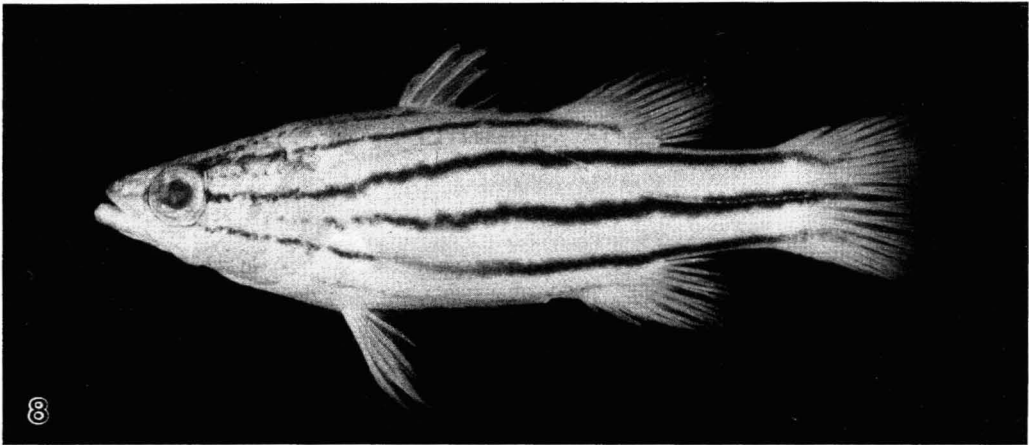
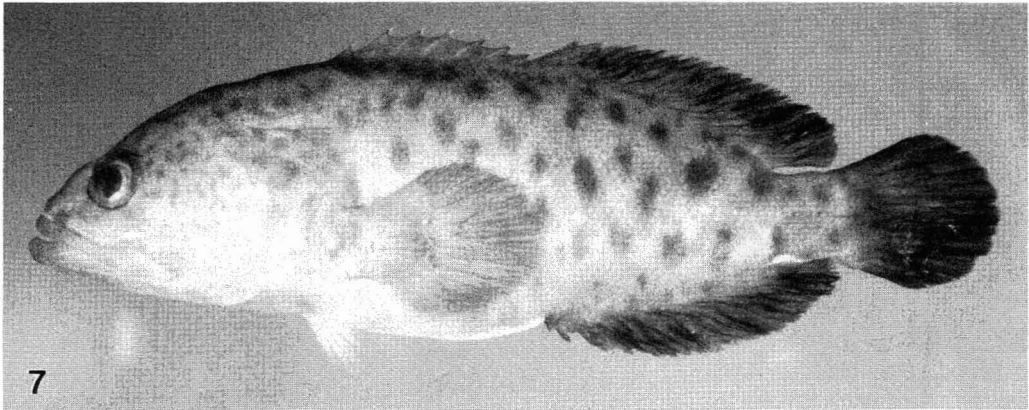
Family LUTJANIDAE

Aprion virescens Valenciennes, 1830

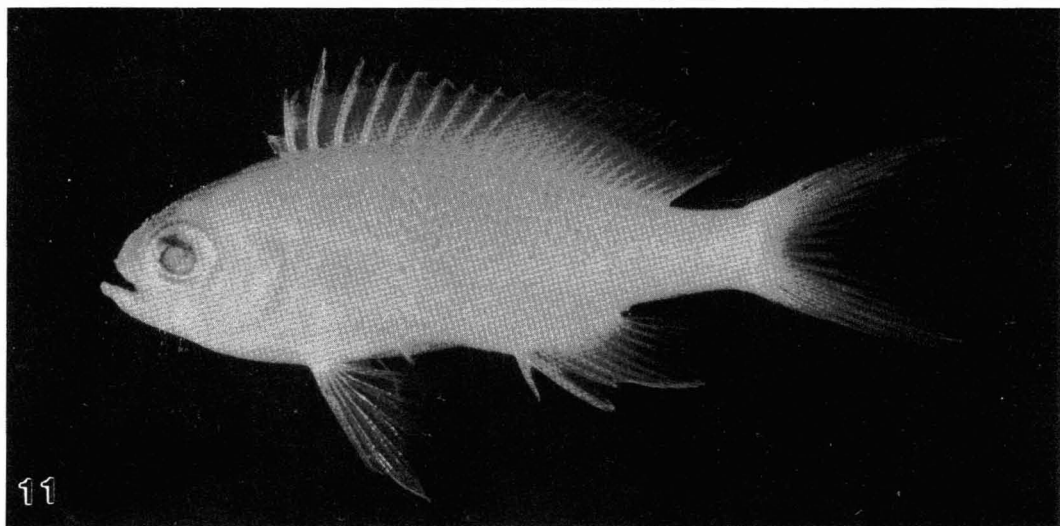
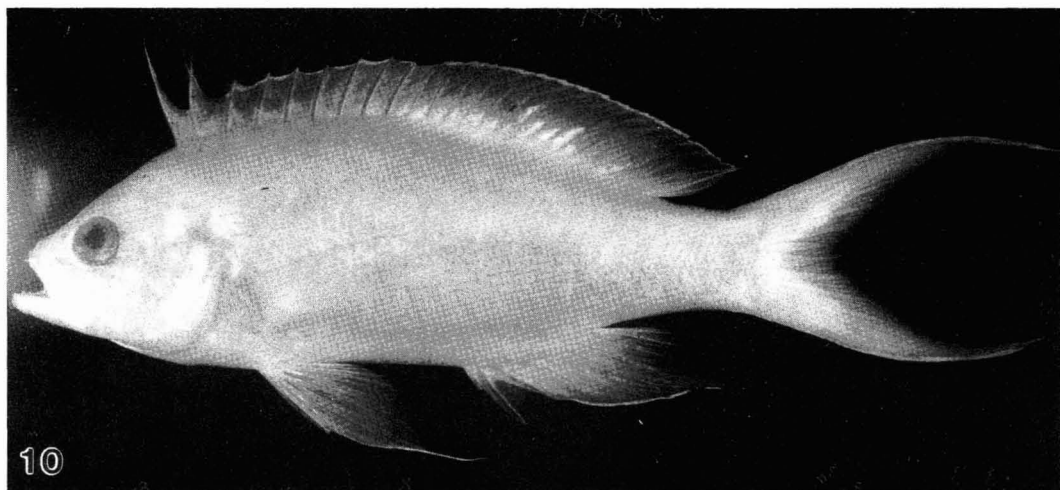
Occasionally caught by local fishermen while bottom fishing in 80–100 m depth outside Donovan's reef (J. Fukumoto, pers. comm.). Specimens or photographs were not available to confirm this record.



FIGURES 4–6. 4, *Brotula multibarbata*, BPBM 34013; 5, *Antennarius coccineus*, BPBM 33971; 6, *Scorpaenopsis fowleri*, BPBM 34008.



FIGURES 7–9. 7, *Aporops bilinearis*, BPBM 33980; 8, *Liopropoma collettei*, BPBM 34000; 9, *Plectranthias winniensis*, BPBM 33937.



FIGURES 10–11. 10, *Pseudanthias bicolor*, BPBM 34002; 11, *Pseudanthias randalli*, BPBM 34001.

Family CARANGIDAE

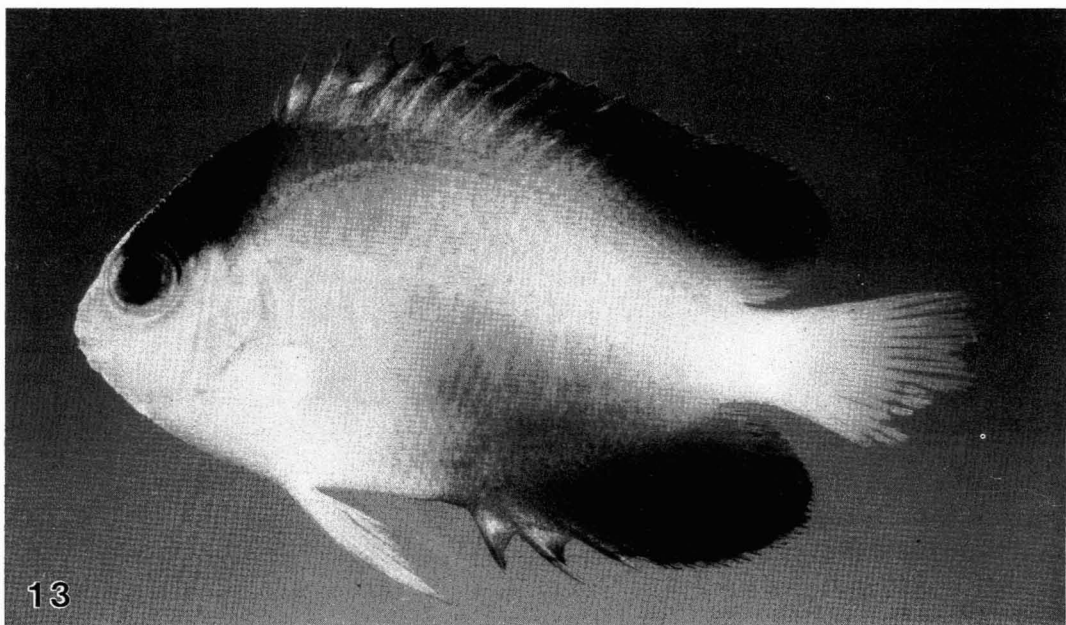
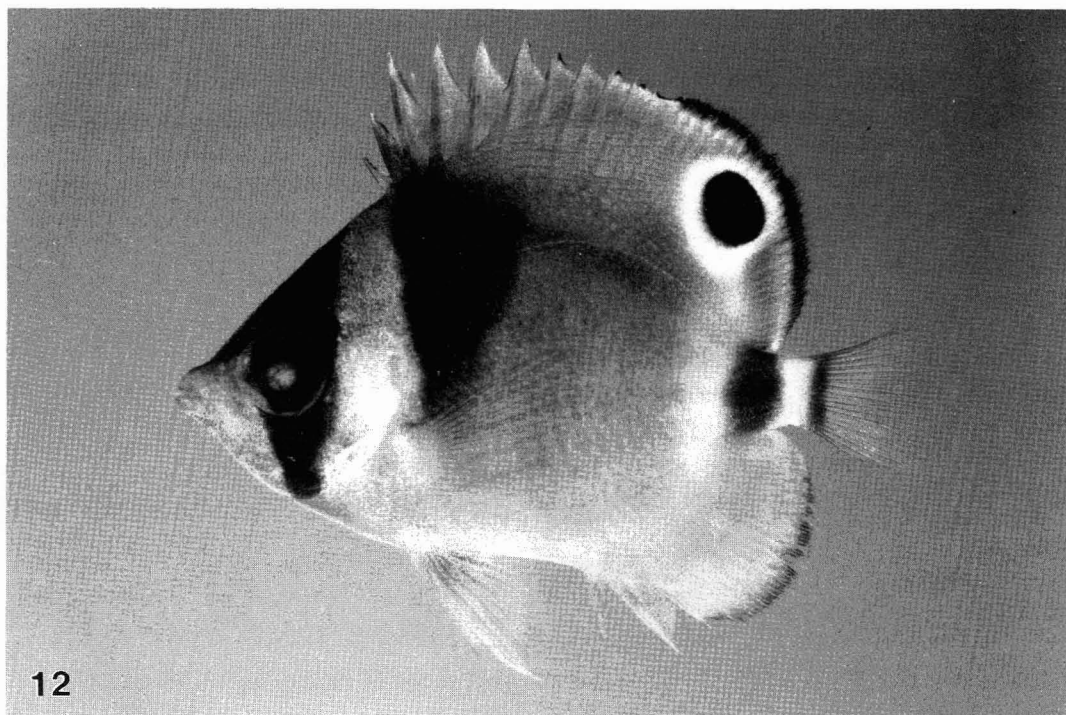
Caranx sexfasciatus Quoy & Gaimard, 1824
BPBM 33938

A single large individual was collected by line fishing in 30 m depth outside the reef. Only the head and tail were preserved; no length measurement was taken. Numerous smaller individuals of this widespread Indo-Pacific species have been seen regularly under the Sand Island pier.

Family CHAETODONTIDAE

Chaetodon lunula (Lacépède, 1803)
BPBM 34027 (1 : 35 mm), Figure 12

A single juvenile specimen of this widespread Indo-Pacific species was collected with hand nets at 10 m depth at the north end of the reef. No other individuals have been seen.



FIGURES 12–13. 12, *Chaetodon lunula*, BPBM 34027; 13, *Centropyge multicolor*, BPBM 33963.

Family POMACANTHIDAE

Centropyge multicolor Randall & Wass, 1974
BPBM 33963 (1 : 46 mm), Figure 13

A single specimen was collected at 45 m depth outside the reef. This species is abundant at similar depths at some island groups of the Pacific such as the Marshall Islands and the Cook Islands, but is known from Hawaii on the basis of a single specimen (BPBM 21059). The Hawaiian and Johnston specimens are probably strays.

Centropyge nahackyi Kosaki, 1989
BPBM 34004 (17 : 29–78 mm)

Centropyge nahackyi is presently known only from Johnston and Hawaii (the latter based on a single specimen, BPBM 32753). The Hawaiian specimen is probably a waif, as a reproducing population of this conspicuous and potentially valuable (to the aquarium fish trade) species is unlikely to have gone unnoticed, given the amount of scientific and commercial diving occurring in Hawaii.

Family POMACENTRIDAE

Abudefduf abdominalis (Quoy & Gaimard, 1824)

Several individuals of this Hawaiian endemic were observed by R. Kosaki and D. Irons at 5 m depth north of North Island. No specimens have been collected.

Family LABRIDAE

Cirrhilabrus luteovittatus Randall, 1988
BPBM 34015 (1 : 73 mm), Figure 14

One male specimen speared at 35 m depth outside the reef. Several other individuals of this Hawaiian endemic have been seen at similar depths at Johnston.

Cirrhilabrus luteovittatus Randall, 1988
BPBM 34016 (1 : 74 mm), Figure 15

One male specimen speared at 30 m depth outside the reef. Described from specimens collected in the Marshall Islands, this species is also known from Truk (Myers 1989) and Pohnpei.

Pseudocheilinus sp.

BPBM 33962 (1 : 40 mm); BPBM 34017 (15 : 30–50 mm)

An undescribed species with an ocellated black spot posteriorly on the side of the caudal peduncle. Known from Cocos-Keeling Islands, Marshall Islands, Cook Islands, and Pitcairn Island. Common at Johnston below 30 m depth, but not known from Hawaii.

Pseudocheilinus evanidus Jordan & Evermann, 1903

BPBM 34055 (3 : 30–40 mm)

Collected with rotenone at 30 m depth outside the reef, but also seen on several occasions at 5 m depth in the lagoon.

Wetmorella albofasciata Schultz & Marshall, 1954

BPBM 34056 (1 : 40 mm)

Known from Africa to Hawaii. Collected with rotenone at 30 m depth, northeast of Mustin Gap.

Xyrichtys pavo Valenciennes, 1839

BPBM 33939 (1 : 165 mm)

Occasionally caught by recreational fishermen bottom-fishing over sand south of Johnston Island at 20–30 m depth. One individual seen by R. Kosaki at 65 m depth north of Mustin Gap. Widespread from the Red Sea to Hawaii and Mexico.

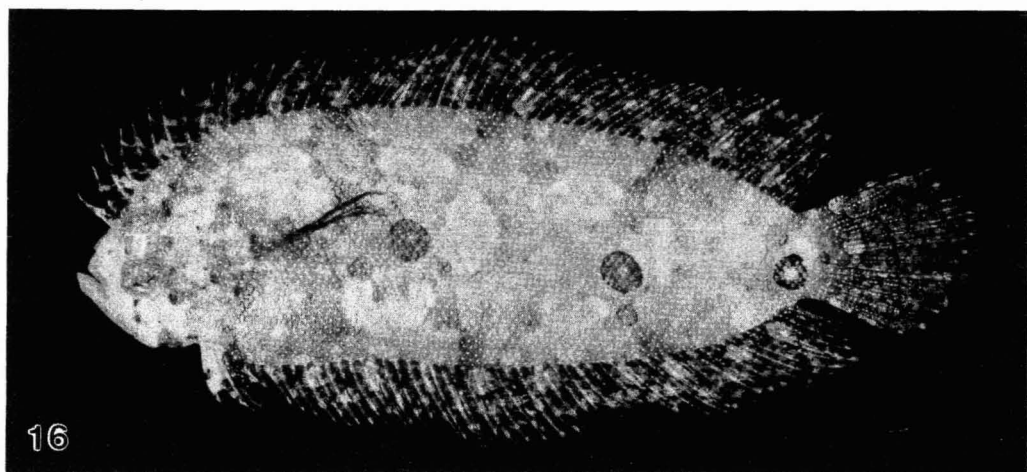
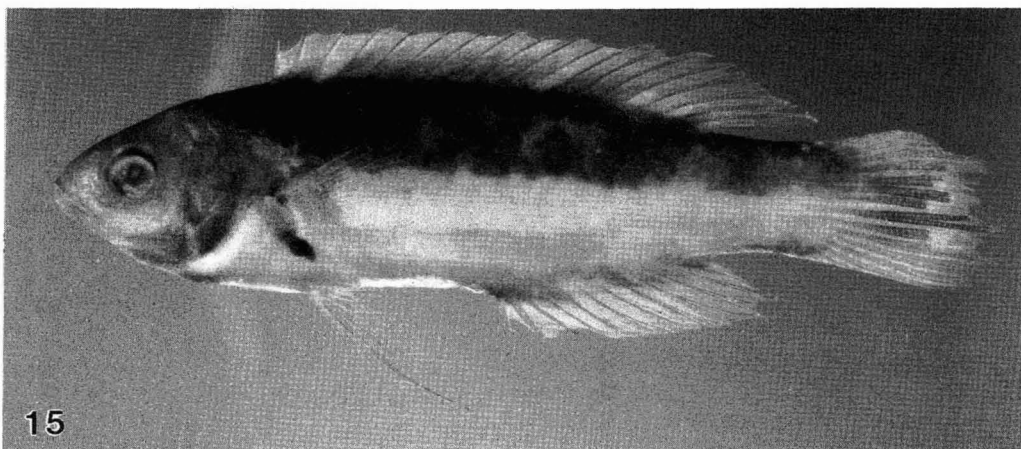
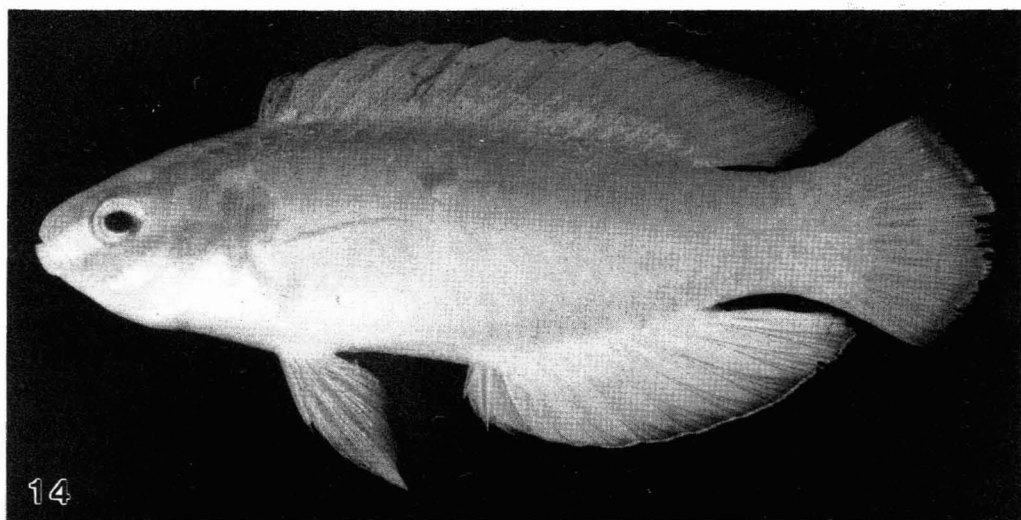
Family ACANTHURIDAE

Naso brevirostris (Valenciennes, 1835)

Observed at close range on numerous occasions by R. Kosaki and D. Irons outside the reef. Loose aggregations of 2–10 individuals are seen up in the water column about 10–20 m from the surface in water 40–60 m in depth. Rarely seen near the bottom during dives, but frequently approached divers during decompression stops.

Naso sp.

Several individuals of an unidentified species of *Naso* were seen outside the reef at 30–50 m depth by R. Kosaki and D. Irons. The fish was not a species of *Naso* previously recorded from Johnston, nor did it fit the description of the unidentified *Naso* seen by



FIGURES 14–16. 14, *Cirrhilabrus jordani*, BPBM 34015; 15, *Cirrhilabrus luteovittatus*, BPBM 34016; 16, *Samariscus triocellatus*, BPBM 34021.

Ralston (described in Randall et al. [1985]). Body shape and size were similar to those of adult *N. hexacanthus*, but no spots were present on the caudal peduncle, and vertical striations were noticed on the body.

Family PLEURONECTIDAE

Samariscus triocellatus Woods, 1966

BPBM 34021 (1 : 41 mm), Figure 16

A single specimen of this widespread Indo-Pacific flatfish was collected with rotenone at 30 m depth outside the reef; several others were seen at rotenone stations between 19 and 30 m depth.

Family TETRAODONTIDAE

Canthigaster coronata (Vaillant & Sauvage, 1875)

This distinctive dark-banded toby was seen by R. Kosaki at the top of a ledge at 65 m depth; one was collected with hand nets but later escaped.

DISCUSSION

Species Composition

The fish fauna of Johnston is depauperate (301 species) when compared with the relatively diverse faunas present in surrounding island groups. Johnston's nearest neighbors, the Hawaiian Islands (which are themselves considered depauperate), are host to over 600 species, and over 800 species are recorded from the Marshall Islands to the southwest. Hawaii and Johnston are located in the path of the North Equatorial Current, whose westerly flow is not conducive to the transport of larvae from the richer areas to the southwest. The 20 most speciose families of fish at Johnston collectively contain 75.6% of the total number of species recorded (Table 1). This is in general agreement with figures of 79% for Christmas Island, Indian Ocean (Allen and Steene 1979), 68% for the southern Great Barrier Reef (Russell 1983), 71% for Guam (Myers 1988), 72.8% for the Marshall Islands

TABLE 1
TWENTY MOST SPECIOSE FAMILIES OF FISHES AT
JOHNSTON ATOLL

FAMILY	NUMBER OF GENERA	NUMBER OF SPECIES	PERCENTAGE OF TOTAL FISH FAUNA
Muraenidae	7	30	10.0
Labridae	19	29	9.6
Acanthuridae	4	21	7.0
Chaetodontidae	4	18	6.0
Holocentridae	5	13	4.3
Serranidae	8	13	4.3
Carangidae	7	11	3.7
Scorpaenidae	6	11	3.7
Ophichthidae	7	10	3.3
Lutjanidae	5	9	3.0
Pomacentridae	4	9	3.0
Pomacanthidae	3	8	2.7
Mullidae	2	7	2.3
Gobiidae*	5	6	2.0
Apogonidae	4	6	2.0
Balistidae	4	6	2.0
Scaridae	2	6	2.0
Monacanthidae	4	5	1.7
Synodontidae	2	5	1.7
Blenniidae	3	4	1.3
Total		227	75.6

*Randall and Hoes (1985) removed the gobioid genera *Nemateleotris* and *Ptereleotris* from the family Gobiidae. Thus, two species of those genera that were listed as gobies by Randall et al. (1985) are not counted among the gobiids in this table.

(Randall and Randall 1987), and 69.9% for Micronesia as a whole (Myers 1989).

These 20 families are among the most speciose at most other Indo-Pacific localities. The species shared between Johnston and each of its surrounding island groups indicate stronger ties to the Hawaiian and Hawaiian/Japanese faunas than to those of the Marshall or Line Islands to the south (Gosline 1955, Randall et al. 1985). Johnston's ichthyofauna has a percentage distribution of the various families (as broken down in Table 1) more similar to that of Hawaii than to those of other central Pacific islands. Gobiidae, which is the most speciose family throughout most of the Indo-Pacific, composes 10.3% of the species of the Marshall Islands (Randall and Randall 1987), a figure typical of most Indo-Pacific localities (Myers 1989). By compari-

son, the gobiids are under-represented at Johnston and Hawaii, composing only 2.0% (six species) and 3.8% (26 species [Hourigan and Reese 1987]) of their respective faunas. In spite of rotenone collections in both shallow and deep water, this study failed to produce any new records in this family, and it seems unlikely that further collecting effort will appreciably increase the number of gobies known to occur at Johnston. The relative isolation of Johnston from surrounding island groups may be a considerable barrier to the dispersal of gobiids, whose demersal eggs yield relatively well-developed larvae (Thresher 1984). Some postflexion gobiid larvae are capable of resisting dispersal by actively remaining in the vicinity of nearshore habitats (Kobayashi 1989). All gobiids recorded from Johnston are also found in Hawaii.

Eels are disproportionately over-represented at Johnston, with ophichthids (snake eels) and muraenids (moray eels) composing 3.3% (10 species) and 10.0% (30 species), respectively, of the fish fauna. By comparison, muraenids compose 5.0% (34 species) of the fauna in Hawaii (Tinker 1978), 4.7% (38 species) in the Marshalls (Randall and Randall 1987), and 3.8% of all Micronesian fishes (Myers 1989). The leptocephalus larvae of moray eels have exceptionally long planktonic lives of up to 10 months (Thresher 1984), making the relative isolation of Johnston less of a barrier to colonization for muraenids than for most reef fishes. Of the 16 central Pacific fishes reaching Johnston but not Hawaii, seven are eels.

Physiological constraints and climatic factors such as warmer ocean temperatures may limit the success of Hawaiian endemics at Johnston (Randall et al. 1985). By the same token, central Pacific fish may be better suited to conditions at Johnston than at Hawaii. Among central Pacific fishes reaching both localities, a number of species that are abundant at Johnston and at atolls farther south are relatively rare in Hawaii. *Centropyge loriculus*, *Chaetodon trifascialis*, *Nemateleotris magnifica*, and *Thalassoma lutescens* are examples. Randall et al. (1985) listed 10 central

Pacific fishes reaching Johnston but not Hawaii, and the present study adds six species to this category (*Gymnothorax margaritophoroides*, *G. zonipectus*, *Siderea* sp., *Pseudanthias randalli*, *Cirrhitilabrus luteovittatus*, and *Pseudochelinus* sp.). Except for a single Hawaiian specimen that is almost certainly a waif, *Centropyge multicolor* could be added to this list.

Endemism and Diversity

Absence of endemism has been noted among the corals (Maragos and Jokiel 1986), crustaceans (Amerson and Shelton 1976), mollusks (E. A. Kay, unpubl. data), and marine flora (Buggeln and Tsuda 1969, Aegeian and Abbott 1985) of Johnston Atoll. Among fishes, three unidentified species (Randall et al. 1985) and one recently described species (Kosaki 1989) are the only possible endemics. However, all are from relatively deep water and may be found at other Pacific islands with more exploration. By contrast, Hawaii has many endemic species of fishes (Hourigan and Reese 1987), corals (Maragos 1977, Jokiel 1987), and mollusks (Kay 1979, Kay and Palumbi 1987).

Lack of habitat diversity may also be a factor limiting fish species diversity at Johnston (Randall et al. 1985). This idea is supported by this study; in spite of efforts concentrating on certain species with habitats lacking on Johnston (e.g., basaltic intertidal species and reef flat species), none were found. However, other factors must also limit species richness and endemism of marine animals at Johnston; even well-represented habitats (e.g., shallow, coral-rich lagoon; spur and groove reef front; deep reef slope) are depauperate.

Other groups of marine animals with less specific habitat requirements are equally impoverished. The shallow marine habitats that are absent at Johnston (estuaries, seagrass beds, reef flats, and basaltic shorelines) are not important coral habitats. Hermatypic corals generally require good water circulation, bright light, and hard substrata upon which to settle. These requirements are well

met at Johnston, and thus low habitat diversity alone cannot explain the low diversity of Johnston's coral fauna (Maragos and Jokiel 1986). Similarly, the deep-water macroalgal diversity at Johnston is low compared to Hawaiian communities in comparable habitats (Aegean and Abbott 1985).

Geological history may have contributed to the present composition of Johnston's shallow-water communities. Habitat area and diversity may have been drastically reduced during temporarily lowered sea levels resulting from Pleistocene glaciations. During those periods of lower sea levels, what is presently the predominant habitat for reef fish (the sheltered, coral-rich lagoon) may have been nonexistent (Figure 17). Wave-cut terraces and ledges at Johnston have been observed at depths of 75 m by divers (R. Kosaki and D. Irons, pers. obs.), and at 60 m (Keating 1985) and 130 m (Ralston et al. 1986) from submersibles, indicating that sea-level drops were more than sufficient to completely expose the 150-km² lagoonal platform, most of which is less than 18 m in depth (Ashmore 1973). A 100-m drop in sea levels at Johnston would expose this platform and reduce shallow-water (< 100 m) habitat area by 93% (based on digitized estimates of habitat areas stratified by depth zones in Ralston et al. [1986]). Sea-level drops during the most recent period of glaciation may have been as great as 150 m (Chappel 1981). Ocean temperature changes were probably not responsible for Pleistocene extinctions at Johnston, as central Pacific surface temperatures during the most recent period of glaciation were not appreciably cooler than they are today (CLIMAP 1976).

The small size of Johnston may contribute to its lack of biotic diversity. Only 25 km in greatest length, with a 15-km side facing the prevailing current, Johnston is a small target for drifting larvae. According to models of the relationship between insular habitat area and species richness (e.g., MacArthur and Wilson 1967), increased extinction rates and decreased immigration rates will result from a decrease in habitat area. These effects should be more pronounced on remote islands than on islands near a mainland or other sources

of potential immigrants. Thus, glacioeustatic reductions of an already small habitat area may have resulted in increased rates of extinction at Johnston.

Isolated atoll populations of shallow-water fish are more vulnerable to extinctions caused by sea-level changes than are high-island archipelago populations of the same species. An atoll's flat top and steep sides would experience a greater reduction in habitat area than the more gently sloping sides of shield-volcano islands. These high islands could thus serve as refuges from which species could re-disperse as sea levels rose (Myers 1989). The Hawaiian Islands, 800 km to the north, are a likely candidate as a source of larvae for re-establishing shallow-water communities at Johnston, as the high degree of endemism among Hawaiian fishes suggests that Hawaii's shallow-water fish faunas were not severely impacted during the Pleistocene. Thus, the Hawaiian affinity of Johnston's shallow-water fish fauna may be due to Hawaii's role as a Pleistocene refuge as well as to prevailing current directions and physical proximity.

The deep-reef communities would not have been as severely impacted by shallow-water habitat reduction and extinctions. The four species of fish that may be endemic to Johnston are all inhabitants of the deep slope, and the only one of these that has been described is most similar to a species common in the Marshall and Society islands (Kosaki 1989). The deep-water (> 100 m) macroalgal communities are not only distinct from the shallow-water communities, but show closest affinities to the deep-water flora of the Marshall Islands (Aegean and Abbott 1985).

Island Integration and Stepping-stones

Rotondo et al. (1981) proposed the island integration hypothesis as a mechanism contributing to endemism in the Hawaiian Islands. According to this hypothesis, islands that formed far to the southeast in the vicinity of the East Pacific Rise may have remained emergent as isolated atolls while the northwesterly movement of the Pacific Plate carried

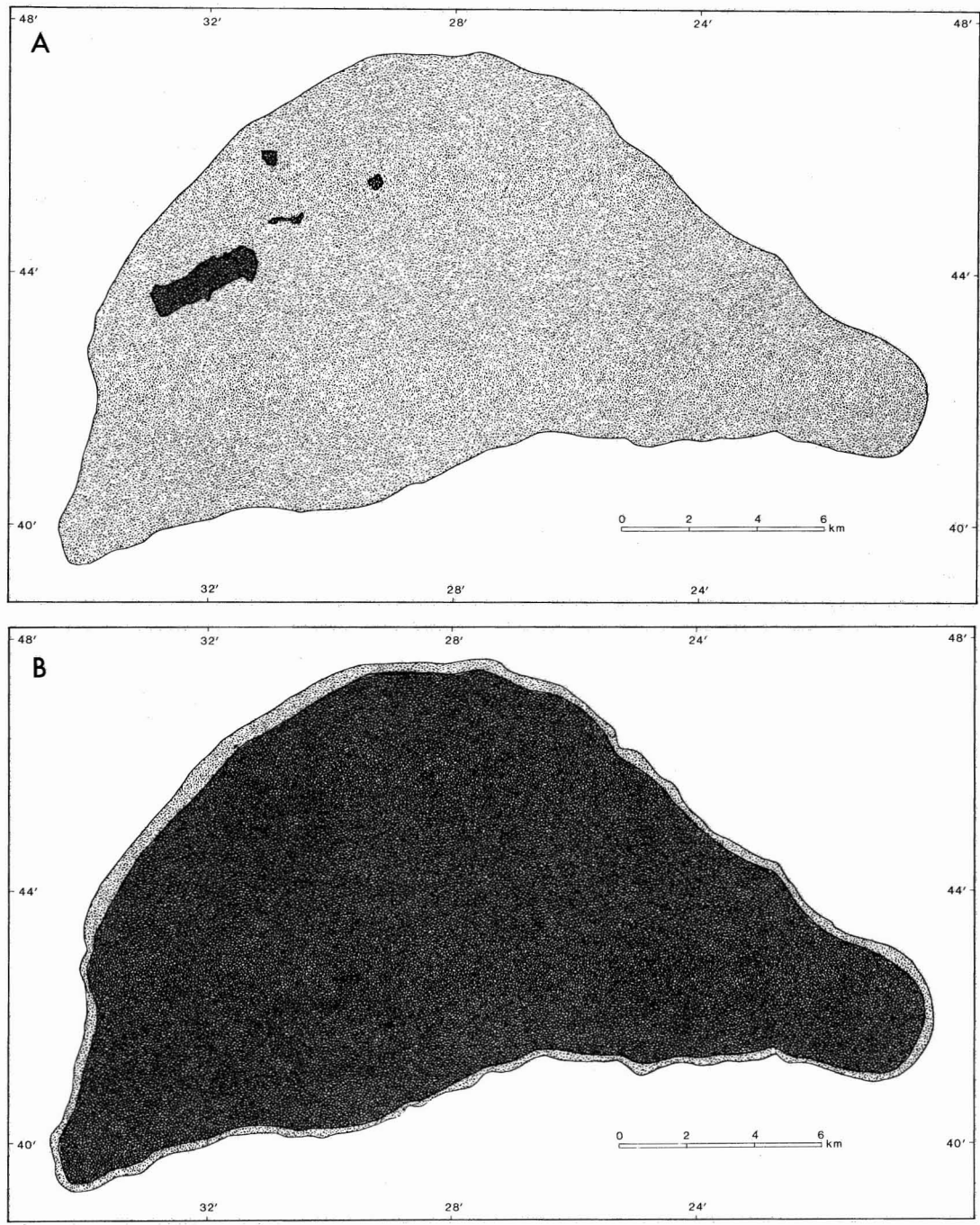


FIGURE 17. Johnston Atoll with sea level at current height (A), and lowered 100 m during periods of Pleistocene glaciation (B). Black areas represent emergent land, and gray areas represent shallow-water habitat (< 100 m depth). During periods of lowered sea levels, the entire top of the atoll platform would be exposed and shallow-water habitat area greatly reduced.

them to the vicinity of the Hawaiian hotspot. Speciation resulting from isolation during that journey, followed by integration into the Hawaiian biota, was suggested as an alternative to the dispersalist explanation invoked by Gosline (1957, 1968) to explain endemism in Hawaiian fishes. Johnston's geological history is similar to the scenario proposed by Rotondo et al. (1981). Johnston formed in an area biogeographically distinct from Hawaii, followed by tectonic transport and isolation en route to its present position. Although Johnston has not become incorporated into the Hawaiian Archipelago, physical integration of volcanic edifices is not necessary for integration of biotas provided that larval transport between islands is possible. Grigg (1981) calculated that two-way exchange of larvae between the Hawaiian Islands and Johnston was possible based on documented current patterns and rates of transport. However, local extinctions related to sea-level changes (discussed above) may inhibit speciation and reduce the ability of a wandering atoll to transport shallow-water fauna between archipelagos.

Springer (1982) listed and discussed several species, subspecies, and sibling-species whose distributions link Hawaii, Johnston, and the islands of the southeast Pacific in a manner consistent with the island integration hypothesis (e.g., the goby *Eviota epiphanes*, known from Hawaii, Johnston, and the Line Islands). Randall et al. (1985) noted that when the distributions of 10 Hawaiian species or subspecies and their closest Line Island relatives are compared, it is usually the Hawaiian subspecies rather than the Line Island form that is present at Johnston. This observation was interpreted to indicate little transport of larvae from the Line Islands to Johnston and is not inconsistent with the island integration hypothesis, which predicts divergence between atoll populations isolated by tectonic events. However, the widespread distributions of most of the species occurring at Johnston make it difficult to speculate on their origins and routes of colonization. Exceptions to this are the small component of Johnston's fauna related to that of southern Japan (via the Northwestern Hawaiian Is-

lands [Randall et al. 1985]) and the Hawaiian endemics that occur at Johnston.

Although it is not geographically or geologically a part of the Hawaiian archipelago, the presence of endemic Hawaiian species at Johnston clearly indicates that it is within the dispersal and successful colonization range of some Hawaiian biota. Slight divergence has been noted between Johnston and Hawaiian populations of *Ctenochaetus strigosus* (Randall 1955), *Scarus perspicillatus*, and the Hawaiian endemic *Labroides phthirophagus* (Randall et al. 1985), suggesting that gene flow between Johnston and Hawaii is restricted. In addition, differences were noted during the present study between Hawaiian and Johnston specimens of two Hawaiian endemics. *Chaetodon multicinctus* from Johnston has less pigmentation in the eye bar (in some specimens it is entirely absent), and *C. tinkeri* has a broader submarginal yellow line on the dorsal and anal fins than Hawaiian specimens.

A number of common Hawaiian endemics have been recorded from Johnston as waifs (*Priacanthus meeki*, *Pervagor spilosoma*, and *Chaetodon miliaris*). Other Hawaiian endemics (e.g., *Pseudanthias ventralis hawaiiensis*, *Abudefduf abdominalis*, *Centropyge potteri*, and *Cirrhitilabrus jordani*) are recorded in extremely low numbers and it is unclear whether they represent numerous waifs (i.e., a small population sustained primarily by occasional, though regular, recruitment from the Hawaiian area) or small but self-sustaining populations. *Abudefduf abdominalis* is known from Johnston only on the basis of a group of adults that was observed in the same location (lagoon north of North Island) for over 4 yr. Their numbers dwindled from five to six individuals in 1986 to a lone individual in 1989, without any apparent subsequent recruitment. This observation suggests a chance colonization event that was not sufficient for successful establishment of this species at Johnston. In any case, the frequent presence of Hawaiian endemics as waifs suggests that transport of their larvae to Johnston occurs regularly (if infrequently), and thus colonization of Johnston by Hawaiian species may be an ongoing process.

Recent introductions of lutjanids to Hawaii provide some insights into the role of island stepping-stones as aids to dispersal. *Lutjanus kasmira*, a snapper introduced to Hawaii in 1955, has spread rapidly throughout the Hawaiian Islands at least as far north as Laysan Island, 1500 km from their site of introduction on Oahu (Oda and Parrish 1981). The presence of seven intervening islands and atolls requires a maximum jump of only 300 km between islands. Although located downcurrent from the Hawaiian Islands, Johnston is separated from Hawaii by open water (800 km from French Frigate Shoals and 1200 km from Oahu) with no intervening islands or reefs to serve as stepping-stones. Four surveys of the fishes of Johnston have been conducted since *L. kasmira* was introduced to Hawaii (Brock et al. 1965, Randall et al. 1985, Ralston et al. 1986, the present study), and recreational fishing and diving have occurred continuously at Johnston since the early 1960s, but *L. kasmira* has yet to be recorded there. It seems unlikely that ecological conditions at Johnston are unsuitable for *L. kasmira* given its wide distribution in the Pacific, its rapid success after introduction in Hawaii, and its generally opportunistic habits. Insufficient recruitment for colonization would, however, explain its absence.

Although Johnston is geologically a part of the Line Islands chain, no emergent atolls or islands currently exist that could serve as stepping-stones between Johnston's fauna and that of the present-day Line Islands 1200 km to the southeast, and Johnston's present geological and biological isolation from the Line Islands has been essentially constant since the Eocene. Seamounts line the Christmas Ridge, which links Johnston and the Line Islands, and dredge or drill samples from DSDP sites 165 and 315 have produced Late Cretaceous reef fossils indicating that at one time they were near the surface (Haggerty et al. 1982). However, based on the fossil record, the tops of these seamounts are thought to have subsided below the photic zone at 65 Ma (Epp 1984). Although seamounts have been suggested as possible stepping-stones for deep-sea fauna (Allison et al. 1967, Grigg and Bayer 1976), they could not play this role for

shallow-water coral-reef biota. The highly irregular subsidence histories of the Line Island volcanos have produced a comparably irregular distribution of emergent atolls. This all but precludes the possibility of the recent existence in the Line Islands of a chain of contemporaneous atolls similar to the Hawaiian-Emperor chain, where island stepping-stones could serve as biotic links between atolls with ages differing by tens of millions of years.

CONCLUSIONS

Although Johnston may once have supported a greater central Pacific faunal component, local extinctions followed by recolonization from the nearest high-island refuge could produce the strong Hawaiian affinity observed at present. Johnston's present fauna may thus be the result of repeated extinctions and recolonization rather than long-term residence of species. Periodic episodes of extinction and recolonization could also inhibit the formation of endemic species. The dominance of widespread species and Hawaiian species may obscure the faunal link to the southeast Pacific predicted by Johnston's geological history.

ACKNOWLEDGMENTS

We are grateful for the assistance of numerous people during the course of this project. C. Balubar, R. Bauer, M. Caballero, T. Evans, J. Hamilton, S. Jazwinski, K. Kavanagh, M. Knecht, and B. Leorna assisted with diving and collecting on Johnston. A. Suzumoto, J. Culp, and T. Hayes assisted in the curation of the specimens. S. Monden prepared the figures. E. A. Kay, M. Kosaki, and R. H. Kuiter provided many constructive comments on early drafts of this paper.

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